Production Biology of Phytoplankton

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LONG-TERM GOALS

To continue to critically and creatively review knowledge about interactions between bulk marine phytoplankton and zooplankton with the hydrographic and chemical environment, as well as the feedback from the biological processes to the abiotic environment. The emphasis is on regional oceanography.

OBJECTIVES

1. To open windows to a largely unknown oceanographic literature by arranging for translations or commissioning new work by Russian-language authors.

2. Review the role of grazing in greatly affecting concentrations of phytoplankton. By way of background, Steemann Nielsen in 1952 introduced the ^{14}C method for measuring photosynthesis of phytoplankton at the low levels often prevailing in the ocean. It was the first rate measurement in biological and chemical oceanography and has had an enormous influence on the field. To celebrate the 50th anniversary, an international symposium, "Phytoplankton Productivity", will be held at the University of Wales in Bangor in March 2002. The thirteen invited lectures by the outstanding colleagues in the field of photosynthesis and phytoplankton physiology will be published prior to the symposium. I observe here that the lectures/papers, of which the abstracts have been distributed, continue along the still prevailing, but somewhat myopic and false line that the primary production of the ocean can be understood merely from phytoplankton physiology and the available resources, i.e., light and nutrients. Too rarely is it realized that primary production per unit volume and time (the rate of interest) is the product of cell division rate (mostly driven by phytoplankton physiology and resources) times phytoplankton concentration, which cannot be derived from measurements of the photosynthetic rate. Moreover, the rate of change of phytoplankton concentration is also a function of the mortality of cells, mostly from grazing.

A principal goal of ecology and, hence, also of biological oceanography is to understand the abundance of organisms and its temporal change. My review will show that Steemann Nielsen did not believe that this goal, in terms of phytoplankton carbon, can be achieved by only measuring and understanding photosynthesis. His principal statements to this effect were made with the open subtropical and tropical seas in mind where phytoplankton concentrations show little seasonal change and where cell division rates are balanced by the losses, among which he thought the grazing to be

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paramount. By four well-suited examples, I will demonstrate in a recently submitted paper that his view holds also for unbalanced situations, specifically, for phytoplankton blooms.

WORK COMPLETED

During FY 2000, most of my time was spent on editing a translation from the Russian of a book about the physiology of plankton, and the completion of a newly commissioned book about a comprehensive Ukrainian Expedition during spring 1990 to the northwestern Arabian Sea. I also wrote a review of the impact of grazing on the development of phytoplankton blooms in the open sea.

RESULTS

Books: 1. The slightly improved version, but heavily edited translation of a 1987 book has been submitted to the printers, the Universities Press (India) in Hyderabad, India:

E.V. Pavlova (1987) *Movement and energy metabolism of marine planktonic organisms.* With 60 figures and 41 tables.

> Author's abstract: The monograph generalizes multi-year investigations on energy metabolism and motility of marine planktonic organisms, from flagellated algae to salps from different regions of the World Ocean. The effect of various factors changing activity and metabolism during experiments is considered. Common features and differences in the character and speed of movement of organisms with different ecology are demonstrated. Data on basal, standard, and total metabolism are compared. Present approaches are considered and new approaches and methods for estimation of metabolism for addressing ecological problems are suggested.

2. K. Banse and S.A. Piontkovski (contributors and editors): *Synoptic Ecosystem Structure of the upper Layers of the Open Northwestern Arabian Sea during the Northeast Monsoon of 1990*. With 184 figures and 29 tables.

> As in most of the comprehensive Soviet and Ukrainian expeditions of the 1980s, the stations of the last Ukrainian cruise to the Arabian Sea were arranged in a "polygon", a grid of 77 stations 55 km apart, instead along a few sections. The contents of the 15 chapters range from hydrography (including calculated vertical velocities and nutrient flux) through heterotrophic bacteria to midwater fishes and squid. The chapters are ready and in the hand of the co-editor for final approval, and only the indexing remains to be done. We plan to submit the manuscript this fall to Universities Press (India).

Papers: 1. A manuscript about the phytoplankton in the offshore region between the southwest coast of India and the Laccadive Archipelago to the west has been accepted and is currently being revised (Proc. Indian Acad. Sci. [Earth Planetary Sci.]):

L.J. Lierheimer & K. Banse: *Seasonal and interannual variability of phytoplankton pigment in the Laccadive (Lakshadweep) Sea as observed by the Coastal Zone Color Scanner.*

> Authors' Abstract: Based on Coastal Zone Color Scanner data of November 1978 through December 1981, the seasonal cycle of phytoplankton pigment in the upper part of the euphotic zone is established for the offshore Laccadive Sea. Year-round, the pigment content is low and the

seasonal range is small, since there are no indigenous phytoplankton blooms; July and August, however, were poorly studied because of the cloud cover of the southwest monsoon. Interannual differences during the northeast monsoon and the spring Transition Period are minor. The abundant phytoplankton caused by the upwelling off India during the southwest monsoon remains essentially restricted to the shelf, but there are occasional large, zonal outbreaks into the Laccadive Sea, as well as others advected to the south of India. Visual inspection of the raw CZCS scenes for June through November 1982–1985, with almost no data until August or even September, shows such outbreaks of pigment-rich water to be common. The role of this discharge from the shelf of the freshwater surplus from precipitation and river runoff, with its nutrients and organic matter including fish eggs and larvae needs to be investigated also with respect to the maintenance of the parent populations on the shelf. Inspection of monthly SeaWiFS images for 1997 through 2000 confirms the absence of indigenous phytoplankton blooms.

2. A manuscript was submitted in September 2001 to Hydrobiologia: Banse, K.: *Steemann Nielsen and the zooplankton* (29 ms. pages, three figures and one table).

Steemann Nielsen's statements about the role of zooplankton, which were largely made with regard to the temporal quasi-equilibrium prevailing in the open low-latitude ocean, are being reviewed. The thrust of the paper is to show that his sentiment also applies to non-static situations, especially phytoplankton blooms. Blooms are caused by the temporary positive imbalance between gain from cell division and loss of cells. Even during the often exponential increase of phytoplankton abundance in blooms, many of the newly formed cells are lost every day, and the rate of net population growth is only a fraction of the particulate net production of the phytoplankton. Specifically, during the blooms in Cushing's North Sea *Calanus* patches of 1949 and 1954 and the two low-latitude iron fertilization experiments (IronEx I, II) of the 1990s, more than half or even most of the newly formed cells were lost daily. These examples are outstanding, because the same water was revisited and dilution and losses by mixing were considered, while sinking was an unimportant loss term, so that grazing was the principal cause of mortality. The examples also show that over the course of the blooms, the rate and even the sign of temporal change of phytoplankton abundance had little relation to the rate of cell division, as already postulated by Riley's 1946 model of the seasonal cycle of phytoplankton on Georges Bank. Thus, in most situations in the open sea and, presumably, large lakes, the rates of cell division (*instead* of photosynthesis by itself) *and* of mortality (most often from grazing) are needed for understanding and predicting the temporal change of phytoplankton abundance. The manuscript also observes that the mechanism maintaining the actual abundance of phytoplankton in the quasi-steady state prevailing over most of the ocean much of the time is still unclear.

IMPACT

1. The translation from the Russian and the newly commissioned book are to open windows to a large body of literature that is largely unknown among English-only speaking scientists. Pavlova's monograph also will be useful for work on freshwater plankton. The book about the Ukrainian expedition and the data now made available on a CD will allow three-dimensional modeling, which is not easily attempted (if at all) based on the JGOFS sections of the mid-1990s. Also, the study will be a time-mark for 1980; without such points-in-time, we cannot establish whether or not the ocean is changing.

2. The review of Steemann Nielsen's opinions about the role of zooplankton is another attempt to get the notion across that mechanistic explanations and the prediction of the concentrations and the temporal changes of phytoplankton must be sought in the context of the plankton as a community, with bottom-up and top-down processes almost always acting together.

RELATED PROJECTS

Collaboration with a few colleagues at India's National Institute of Oceanography in Goa and the Central Marine Fisheries Research Institute in Cochin continues. The focus is on the stability on the decadal scale and the short-term variability of the offshore oxygen minimum of the Arabian Sea and on the near-bottom oxygen concentration on the shelf of the Indian west coast during the southwest monsoon. We are using existing data.

PUBLICATIONS
(see also under Results, above)

Banse, K. (in press) *Bruce W. Frost - an appreciation.* Hydrobiologia (11 ms. pages for a volume on the occasion of his 60th birthday).